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Review

# Reproducing reproduction: How to simulate mast seeding in forest models

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## ABSTRACT

Masting is the highly variable and synchronous production of seeds by plants. Masting can have cascading effects on plant population dynamics and forest properties such as tree growth, carbon stocks, regeneration, nutrient cycling, or future species composition. However, masting has often been missing from forest models. Those few that simulate masting have done so using relatively simple empirical rules, and lack an implementation of process-based mechanisms that control such events. Here we review more than 170 published papers on mechanistic formulations of masting, and summarize how the main processes involved in masting and their related patterns can be incorporated in forest models at different degrees of complexity.

Our review showed that, of all proximate causes of masting, resource acquisition, storage and allocation were the processes studied most often. Hormonal and genetic regulation of bud formation, floral induction, and anthesis were less frequently addressed.

We outline the building blocks of a general process-based model of masting that can be used to improve the oversimplified functions in different types of forest models, and to implement them where missing. A complete implementation of masting in forest models should include functions for resource allocation and depletion, and for pollination, as regulated by both forest structure and weather in the years prior to seed production. When models operate at spatio-temporal scales mismatched with the main masting processes, or if calibration data are not available, simulation can be based on parameterizing masting patterns (variability, synchrony, or frequency). Also, observed masting patterns have the potential to be used as "reality checks" for more process-based forest models wishing to accurately reproduce masting as an emergent phenomenon.

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## 1. Introduction

Understanding forest ecosystems and predicting their dynamics through models remains an abiding concern of forest researchers. Modeling forest dynamics using only a limited set of fundamental variables represents a challenging task, considering the myriad of components, mechanisms and the degree of complexity involved. Models, however, provide invaluable information to plan sustainable forest management (Monserud, 2003; Taylor et al., 2009). In order to improve the accuracy of forest models operating under changing environmental conditions, ecological processes which have big effects on forest dynamics must be accounted for.

A prominent but overlooked example of such processes is mast-seeding or masting, i.e., the highly variable and synchronous production of seeds by a population of plants. Masting occurs among grass, shrub, and tree species in many different biomes (e.g., Schauber et al., 2002; Abrahamson and Layne, 2003; Poncet et al., 2009; Drobyshev et al., 2010). The synchronized annual variability displayed by masting has been explained by several hypotheses (Sork, 1993; Kelly, 1994; Herrera et al., 1998; Kelly and Sork, 2002). Masting events are thought to be "cued" by particular climatic conditions synchronized over large areas (i.e., Moran effect) in the years that precede flowering (Schauber et al., 2002; Piovesan and Adams, 2001, 2005; Kelly et al., 2013). However, no general consensus has been reached yet on the complete set of processes and mechanisms causing masting (Pearse et al., 2016). Masting is intimately related to other processes of forest dynamics (Fig. 1), such as tree growth (Thomas, 2011; Muller-Haubold et al., 2013; Hacket-Pain et al., 2017), seed dispersal, and regeneration (Vander Wall, 2001; Ascoli et al., 2015). The relative contribution of seed production to annual net primary productivity (NPP) in masting species has been estimated for some species at between 20% and 57% (Mund et al., 2010; Muller-Haubold et al., 2013), and about 15% of stem biomass growth (Mencuccini et al., 1995).The fact that tree growth is reduced in years of heavy seed production (Piovesan and Schirone, 2000) may help to explain the failure of most process-based forest models to reproduce observed inter-annual variability in carbon fluxes or observed biomass growth (Drobyshev et al., 2010; Collalti et al., 2016), as well as the disagreement between modeled growth-climate relationships and observed tree rings (Babst et al., 2013).

Additionally, masting has far-reaching effects on ecosystem functions and services, such as carbon sequestration (Miyazaki, 2013), and on community trophic cascades, including birds and mammals (Ostfeld et al., 1996; McShea, 2000; Clotfelter et al., 2007; Jensen et al., 2012; Zwolak et al., 2016; Selås, 2017) and vectors of human diseases (Ostfeld, 1997; Tersago et al., 2009).

In forestry research, forest models are sets of equations that integrate several mechanisms describing and predicting important forest processes, such as growth, mortality and regeneration (e.g., Monserud, 2003; Vacchiano et al., 2012). Since masting has such widespread influences on forest ecosystem dynamics, implementing it into predictive forest models may contribute to improve their accuracy, not only in terms of modeling seed production but also extending to growth trade-offs, pollen and seed dispersal, establishment success, species migration, cascading trophic interactions, effects of silvicultural treatments, and ecosystem resilience to natural disturbances or climate change. In some of these forest models, seed production has been implemented either as a constant or limitless process, not integrated into allocation (Price et al., 2001), or, more realistically, as a function of NPP or leaf mass (e.g. Bossel, 1996) – however, this is unlikely to fully reproduce the characteristics of masting. Those that did attempt to model masting explicitly used a simplistic implementation, e.g., a regular frequency of years with high seed output (Rammig et al. 2007), neglecting the relationship between masting processes and environmental conditions. Overall, masting has been included in forest models in very few cases (Table 1), be it to look specifically at masting effects, or within large-scale forest ecosystem models in which patterns of seed production have not been specifically developed to incorporate mast seeding.

Inconsistent study design, omitted reporting of effect sizes, and lack of validation of model prediction against observed data mean that no conclusive evidence exists on whether an explicit inclusion of masting in forest models is relevant to accurately predict ecosystem and ecological dynamics. The effect size of including/not including masting in models could possibly vary depending on the desired output variable and on the spatial and temporal span being modeled (e.g., an individual stand vs. a regional forest landscape). Rigorously validated analyses of the accuracy of forest model prediction with and without masting are greatly needed. However, the inclusion of masting in forest models can be crucial on one side for greater realism, and on the other to

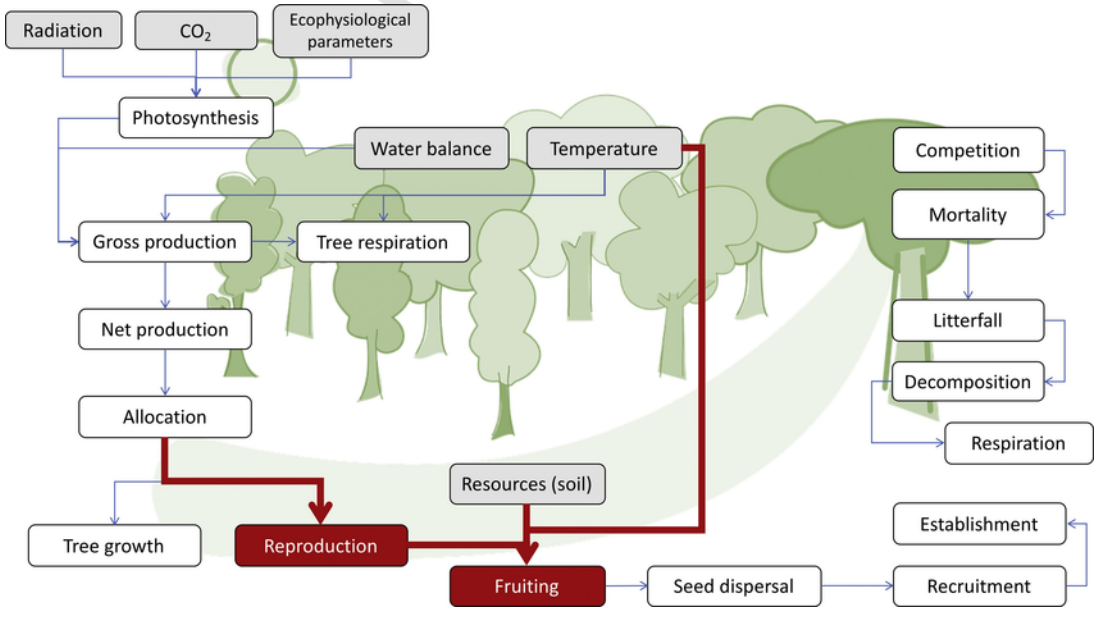


**Fig. 1.** Simplified process diagram for a generic forest model. Grey boxes: input variables, white: processes, orange (and red arrows): masting-related processes (modified from Fischer et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Forest models analyzing the effect of masting on forest dynamics.

| Model | Scope | Functional group or species/Biome | Reference | Did masting have an effect? |
|---|---|---|---|---|
| Models dealing with the effects of masting | | | | |
| Individual based gap model (FORMIND) | Effect of masting on forest structure | Broadleaf/Tropical | Köhler and Huth (2004) | Yes: Masting affected the population dynamics of small trees |
| Gap model (SAL) | Effect of masting on tree species range shift | Broadleaf evergreen and broadleaf deciduous/Tropical and temperate | Kohyama (2005) | No: null effect or slightly delayed tree migration speed |
| Individual-based tree and seed predator model | Effect of masting on rodent population dynamics | Simulated species (based on temperate broadleaf) | Tamburino and Bravo (2013) | Yes: masting lowered the average number of seed predators per tree |
| Vegetation model + individual based tree regeneration model | Effect of seed production on forest succession of wind disturbed forests | Conifer/Subalpine | Rammig et al. (2007) | Yes: mast frequency and timing affected regeneration response to disturbance |
| Other forest ecosystem models | | | | |
| Gap model (FORSPACE) | Effects of climate change on long-term forest dynamics | Conifer and broadleaf/Temperate | Kramer et al. (2006), Kramer et al. (2008) | Yes: mast years were associated with increased dispersal distances |
| Individual based gap model | How spatiotemporal processes shape treeline patterns | Conifer/Temperate | Wallentin et al. (2008) | Unknown: Fecundity is an important driver but specific role of masting not reported |
| Dynamic Global Vegetation Model (LPJ-DISP) | Past plant migration refugia | *Fagus grandifolia*/Temperate to Boreal (virtual landscape) | Snell and Cowling (2015) | Yes: Masting increased the number of long-distance dispersal events |

equip models with a process-based understanding that would enable to produce projections out of the range of their calibration domain, e.g., under climate change.

In the following paragraphs, we first provide a concise overview of the most important patterns and processes related to masting. Then, we propose ways to implement them in forest models across different spatial, temporal, and ecological scales. To do so, we carried out a review of formulations used in the scientific literature to model masting patterns and processes. Finally, we bring this evidence together in a broader discussion on what to consider when implementing masting in forest models.

## 2. Masting patterns and underlying processes

Masting can be modelled using two main approaches: (a) reproducing demographic and ecological patterns produced by masting (both spatially and temporally), or (b) understanding and reproducing mechanistic processes (or "proximate causes" *sensu* Kelly, 1994), which is usually a more complex task and not necessarily leading to less uncertainty than the former.

### 2.1. Patterns

Patterns of masting have been characterized in different ways in the literature (e.g., Kelly and Sork, 2002; Koenig et al., 2003; Pearse et al., 2016). Here we refer to variability, synchrony, and frequency as key elements to describe masting patterns (Fig. 2), although other elements have been proposed, such as temporal autocorrelation (e.g., Koenig et al., 2003; Crone et al., 2011).

- Variability: defined as the absolute or relative difference in the number or mass of seeds produced by one unit (typically a tree or stand) across time (e.g., Herrera et al., 1998; Greene and Johnson, 2004; Richardson et al., 2005; Crone et al., 2011). Seed production that is either large or zero produces a bimodal frequency distribution of seed crop size (but see Allen et al., 2012). For more continuous distributions, variability can be quantified either by the coefficient of variation (CV) of the number of seeds produced across time, or by the recently proposed "disparity index" (Fernández-Martínez et al., 2017a). The latter is a modification of CV that does not depend on the mean, and takes into account actual year-to-year variation in a temporally explicit way. A particular type of variability often found in masting species is a negative autocorrelation: the current seed crop can be often explained, to a high degree, by a negative correlation with the previous year's crop (e.g., in alternate bearing species, or as a consequence of resource depletion).
- Synchrony: defined as the degree of similarity between the number or mass of seeds produced by a population of trees or stands at the same time, for one or multiple species (e.g., LaMontagne and Boutin, 2007; Fearer et al., 2008; Allen et al., 2012). The spatial extent of synchrony may range from stand to region or even sub-continent (Koenig and Knops, 2000); a marked distance-decay in synchrony was reported at continental (Vacchiano et al., 2017), regional (e.g., Fearer et al., 2008), and local (e.g., Allen and Platt, 1990) scales. Synchrony can be measured at the individual level (correlation between individual and population seed production) or at the population level (correlation among trees or stands, or percentage of trees or stands showing a similar seed output).
- Frequency: defined as the number of high seed production years during a time period (e.g., Sork et al., 1993; Greene and Johnson, 2004; Allen et al., 2012). When the causes for synchrony and variability are explicitly modeled, frequency is an emergent behavior, and regular cycles in fruiting need not to be mechanistically explained. However, they can and should be linked to the temporal patterns of the underlying drivers, e.g., solar activity or climate oscillations (Ascoli et al., 2018). In this review, we consider frequency as a stand-alone pattern, because the question of interest usually is "when will the next massive fruiting occur?". Furthermore, masting frequency is typically the only parameter that has been implemented in forest models thus far (e.g., Rammig et al., 2007).

### 2.2. Processes

The causes driving variability and synchrony in seed production have been categorized as ultimate and proximate (Pearse et al., 2016). Ultimate causes include processes associated with evolutionary timescales, such selective pressure; they are excluded from the present review because they would be incompatible with the time-span covered by most forest models used for ecological or forest management prediction.

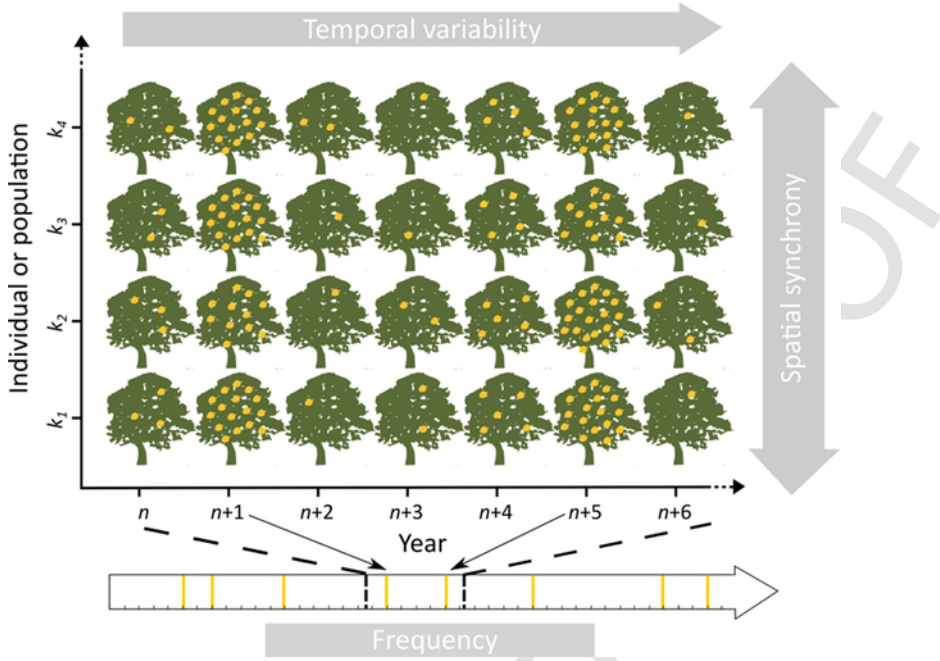


**Fig. 2.** Annual patterns of masting in a tree species. Masting is generally defined by three main aspects: (1) a high temporal variability of seed production at individual or population level, (2) a high spatial synchrony of seed production through time among individuals of a same population, and (3) a non-regular frequency of years of high seed production (yellow bars). The number of seeds produced per year is represented for one individual or population ($k_i$) through time in yellow. Frequency is illustrated at the bottom as the number of years of high seed production such as (n + 1) or (n + 5) in a certain time period (can be high or low depending on the time period chosen). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Proximate causes, on the other hand, operate between a decade and a few days before seed production. They include dynamics of resource accumulation and depletion, weather events favorable to phenological phases involved in flowering and fruiting, and all cellular and genetic processes involved in their occurrence (Crone and Rapp, 2014; Pearse et al., 2016). Masting patterns emerge when several proximate causes interact across space and time, affecting all processes that lead to seed production: resource acquisition, bud initiation, anthesis, pollination and fertilization, flower abortion, and seed maturation (Allen et al., 2017) (Fig. 3).

*2.2.1. Resource acquisition, storage and allocation*

Trees allocate resources to growth, survival, and reproduction (cf. Fridley, 2017 for a review). It is well established that there is an internal cycling of resources (see Millard and Grelet, 2010 for a review on carbohydrates and Nitrogen [N]; and Proe and Millard, 1995 for Phosphorus [P]) and that macronutrients influence fecundity and seed production (Reekie and Bazzaz, 1987; Ichie and Nakagawa, 2013; Miyazaki, 2013; Han et al., 2014). Yet it is still unclear which of the nutrients – non-structural carbohydrates (NSC), N, or P – and interactions among nutrients (compensation effects) – are most limiting for reproduction (Körner, 2003; Han et al., 2008; Sala et al., 2012), whether nutrients used for reproduction come from recently acquired or accu-

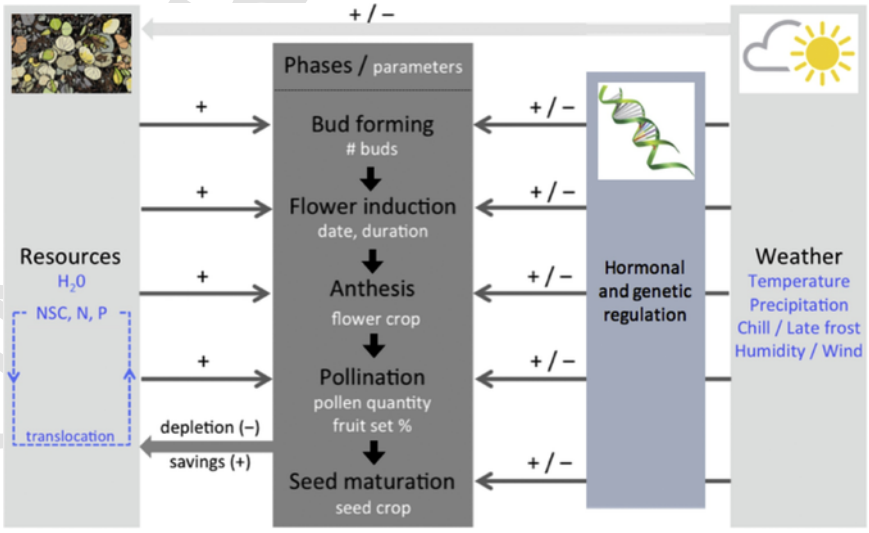


**Fig. 3.** Functional links between processes leading to masting and their proximate causes (+: positive correlation, –: negative) (modified from Pearse et al., 2016).

mulated resources (Koenig and Knops, 2000; Kelly and Sork, 2002; Sala et al., 2012), and in the last case what is the accumulation period (Ichie et al., 2018). Until today, four non-mutually exclusive mechanisms have been proposed to explain how resource supply and uptake are involved in seed production:

- "resource matching", in which a fixed fraction of resources is allocated each year to reproduction (Koenig and Knops, 2000);
- "storage", in which trees accumulate resources over several years in order to eventually allocate them to high seed production, leading to negative temporal autocorrelation in seed production series (Sork, 1993; Koenig et al., 1994);
- "switching", in which a variable fraction of resources is allocated each year to reproduction leading to negative correlations between reproduction and growth (Yasumura et al., 2006; Monks and Kelly, 2006; Sala et al., 2012);
- "veto", in which some external agent (e.g., late frost) may limit the investment in fruiting, preventing resources to be allocated to reproduction (Koenig et al., 2015; Pesendorfer et al., 2016; Bogdziewicz et al., 2017b).

#### *2.2.2. Hormonal and genetic regulation of bud formation, floral induction, and anthesis*

Floral induction is driven by hormonal induction, which incorporates the influence of numerous external and internal cues (Bernier and Périlleux, 2005; Turnbull, 2011; Bluemel et al., 2015). Large seed quantities are directly correlated to gibberellin contents (Böhlenius et al., 2006; Turnbull, 2011), whereas fruit abortion is driven by ethylene (Bleecker and Kende, 2000). The biosynthesis of growth hormones (Wahl et al., 2013) and the expression of flowering genes (Miyazaki et al., 2014) are stimulated under higher resource supply, especially N (Sedgley and Griffin, 1989).

#### *2.2.3. Pollination*

A tree can produce a large quantity of seeds when three conditions are met: (i) the tree produces a high initial flower crop, (ii) pollination success is high, and (iii) a high proportion of fertilized flowers mature into fruits. Most masting species are outcrossers (Pearse et al., 2016). Therefore, masting is restricted by pollen production by other plants in the population (Smith et al., 1990). Plants with many pollen-producing neighbors produce larger seed crops than more isolated ones (Knapp et al., 2001). Theoretical models showed that such density-dependent pollen limitation ("pollen coupling") can also induce synchrony in seed production (Isagi et al., 1997; Lyles et al., 2015; Venner et al., 2016). However, empirical support of the role of pollen limitation on masting remains scarce, and the importance of pollen limitation as a trigger of seed production is still widely debated (Koenig and Ashley, 2003; Koenig et al., 2012; Rapp et al., 2013; Pearse et al., 2015; see also Pearse et al., 2016 for a review).

#### *2.2.4. Seed maturation: fertilization and flower abortion*

In perennial plants, fertilized flowers are often aborted (Stephenson, 1981; Sork and Bramble, 1993; Holland et al., 2004). From an evolutionary point of view, flower abortion is an inexpensive strategy to either maximize the long-term quality of the remaining fertilized flowers (Becerra and Lloyd, 1992), or re-allocate resources to other non-reproductive processes in response to unpredicted disturbances (Goubitz et al., 2002; Montesinos et al., 2012), especially when resources are depleted during fruit maturation (Tsuruta et al., 2011).

#### *2.2.5. Weather: cues and vetoes*

Many of the processes above are influenced (linearly or not: Fernández-Martínez et al., 2017b) by weather, as confirmed by the large number of studies reporting on correlations between weather and seed production in masting species (Allen et al., 2014; Canham et al., 2014; Moreira et al., 2015; PérezRamos et al., 2015; Caignard et al., 2017; Vacchiano et al., 2017). Acquisition and storage of resources depend on photosynthesis and on the amount of solar radiation, but are also constrained by water limitation and drought stress, which were shown to affect seed crops with a lag of two or three years (Newbery et al., 2006; Smaill et al., 2011; Barringer et al., 2013; Muller-Haubold et al., 2013; Bachofen et al., 2017). Other studies highlighted a correlation between large seed crops and higher than average summer temperatures during both floral initiation and fruit maturation (Piovesan and Adams, 2001; Richardson et al., 2005; Fearer et al., 2008; Buechling et al., 2016), which can also be attributed to resource-mediated mechanisms.

Meteorological conditions (solar radiation and temperature) can also affect flowering-inducing hormones such as gibberellins and phytocromes (reviewed by Ruan et al., 2012), and have a crucial impact on pollination. In particular, pollen concentrations are negatively correlated to rainfall and humidity but positively correlated to temperature during the pollen season (Cecich and Sullivan, 1999; Sabit et al., 2016; Bogdziewicz et al., 2017a). The pollen season itself is longer under drier and warmer weather (Fuhrmann et al., 2016). Also, spring microclimatic conditions affect the local budburst synchrony (that is a proxy for flowering synchrony and pollen availability) and consequently the pollination efficiency (Koenig et al., 2015).

Finally, extreme weather events can damage reproductive structures by e.g. late frost during flowering (Augspurger, 2009; ChangYang et al., 2016) or intense summer rainfall during fruit maturation (Abrahamson and Layne, 2003). However, the variability of weather has been shown to be often smaller than the variability in masting, indicating that climate alone cannot explain all variability in masting (Koenig and Knops, 2005).

## 3. Literature review

The scope of this review is to summarize how masting patterns and processes have been described in the scientific literature. This includes quantitative analyses of masting variability, synchrony and frequency, as well as empirical or process-based models of processes leading to masting at all ecological levels and geographic scales. To do so, we searched the Scopus database for titles and abstracts containing the following search string: ((masting OR "mast seeding" OR "mast fruiting" OR "mast flowering") AND (variability OR pattern OR synchrony OR periodicity OR model* ) AND (forest OR tree)). We complemented the search results by a targeted search based on references from a recent and comprehensive review on masting processes (Pearse et al., 2016). The geographic scope of our search was global.

We excluded from the analysis papers that only reported masting observations without quantitatively describing a pattern or modeling a process. Out of a total of 360 papers found for the period 1957–2016, we selected 206 for further analysis, containing a total of 323 individual model formulations for a pattern, a process, or both (i.e., several papers contained more than one pattern and/or process).

For each individual model formulation, we collected information regarding the modeled species, the pattern and process being modeled, and the modelling methods (Table 2).

The largest share of studies was carried out in temperate ecosystems (n = 105; 51%), followed by studies from Mediterranean (17%), tropical (13%) and boreal biomes (5%). Only 11 papers referred to multiple biomes, reflecting the overall scarcity of generalized approaches on masting (Fig. 4a). Most studies involved broadleaves (n = 140) and, more in general, wind-pollinated species (n = 130 with exclusive anemophilous pollination), a strategy that is disproportion-

**Table 2**
Information collected for each masting formulation in the literature review.

| Data collected | Explanation |
|---|---|
| Pattern | Variability, synchrony, frequency |
| Process | Resource dynamics, anthesis and flower induction, pollination, abortion and seed maturation, hormonal induction and genetics, weather |
| Ecological level: the hierarchical level of ecological and data complexity at which masting is addressed. | Descriptive: if only a pattern is reported without any explicit cause. Weather cues fall in this class. |
| | Demographics: numerical oscillations of reproductive organs (flowers, pollen, fruits, seeds)[a]. |
| | Resource: processes that build up and consume macronutrients (NSC, N, P) or water |
| | Biochemical: processes mediated by inter-cellular (non-structural carbohydrates, hormones) and intra-cellular pathways (enzymes, mithocondrial activity) |
| | Genetics: processes related to gene expression, and regulation |
| Mathematical complexity: the type of formulation used to model masting pattern or process | Empirical observation: a non-statistical comment, observation or association, based on empirical evidence presented in the paper |
| | Constant: an invariant value |
| | Distribution: a value extracted from a probability or frequency distribution |
| | Uni- and multivariate: a mathematical relationship (correlation, regression…) |
| | Linking seed production to one or more predictors. |
| Stand-alone | Whether the model formulation was the main analytical tool of the paper, as opposed to a series of chained formulations that may or may not end with seed production as output variable |
| Empirically-based | Whether the algorithm was based on empirical data or on theoretical or conceptual models |
| Response and explanatory variables | Categories of predictor and response variables being measured |
| Spatial unit: spatial grain at which the algorithm is run, and number of sampling units observed or measured | Leaf, organ, tree, stand, population, super-population |
| Geographical focus: the spatial extent of the study | Stand, region, country, multi-country, continental, species range, global |
| Temporal unit: temporal step at which the algorithm is run, and number of observations or measurements in time | Hour, day, month, year, decade |
| Biome: bioclimatic area in which the algorithm is run | Boreal, temperate, mediterranean, or tropical |
| Species group | Conifers, deciduous broadleaves, evergreen broadleaves, o others |
| Seed dispersal strategy | Anemochorous, zoochorous, hydrochorous, barochorous |
| Pollen dispersal vector | Wind, insects, other animals, water |

[a] Several studies have found a positive correlation between seed abundance and flower, pollen and fruit abundance (Schauber et al., 2002; Pidek et al., 2010; Kasprzyk et al., 2014; Ascoli et al., 2015). Notably, the quantity of pollen directly affects pollination efficiency and thus the percentage of sound seeds (Nilsson and Wastljung, 1987; Norton and Kelly, 1988; Koenig et al., 2015). Small discrepancies between flower, pollen, and seed abundance may occur in presence of flower abortion and pollination failure.

ately common among masting species (Herrera et al., 1998) especially for cross-pollinating ones (Satake and Iwasa, 2000, 2002a,b).

The dominant geographical focus was the stand (47% of all papers), followed by region (31%); at the two ends of the spectrum, both individual-tree and continental/global algorithms were varey rare (4% and 2% respectively). The temporal unit was almost always the year (90%), with only 16 studies having a monthly time resolution or finer. Most analyses were conducted at tree (51% of all papers), stand (26%), or population level (20%) as spatial units. The predominant level of ecological and data complexity at which masting was described or modelled was demographics (52%), i.e., the numerical oscillations of reproductive organs (flowers, pollen, fruits, seeds) and their environmental drivers. One in five studies (22%) had a merely descriptive character, i.e., no causal or correlative analyses were carried out for the masting patterns reported. Studies explicitly looking into resource dynamics or finer-scale processes were 20% of the total.

Of all 323 masting formulations covered in our review, most (77%) described variables related to seeds or fruits, which are usually easier to measure and more directly related to masting than e.g., pollen or flowers (Fig. 4b). A small group of resource-based formulations instead modeled the nutrient content of tree organs, including reproductive ones, following masting. Response variables were more often described by univariate (41%) or multivariate (31%) algorithms.

The complete review table and metadata is reported as Supplementary material S1.

### 3.1. Patterns

Variability was the most frequently analyzed pattern (60%, 194 of 323 formulations,), vastly exceeding synchrony (17%) and frequency (11%) (Fig. 4b). By definition, synchrony was the only pattern where the geographical focus was always larger than a single tree.

Variability was usually quantified using the coefficient of variation of masting time-series series (e.g., Ichie and Nakagawa, 2013; Monks and Kelly, 2006), or the standard deviation (e.g., Nussbaumer et al., 2016) or variance (e.g. Koenig et al., 1994) of the time-series. Other methods to quantify variability included the temporal autocorrelation structure in the data (e.g. Koenig et al., 2003).

Some studies extended the analysis by linking variability in seed production with variability in weather conditions, usually using a correlation-based approach (e.g., Selås et al., 2002; Kelly et al., 2013). Typically, strong correlations were found with weather measured in seasons associated with masting-related processes; multiple regression models could reproduce the observed variability of reproduction with a high accuracy (Poncet et al., 2009; Vacchiano et al., 2017). A variation on this theme is to relate variability to teleconnection indices rather than climate indices (Schauber et al, 2002; Sakai et al., 2006; Ascoli et al., 2018). A second group of studies attempted to explain observed variability in seed production using information on biological processes (e.g., flower and leaf phenology) (Koenig et al., 2012; Pesendorfer et al., 2016).

Synchrony between populations was modeled by correlating it to geographic distance (e.g. by Mantel tests: Suzuki et al., 2005) or by using indices of spatial aggregation (Fredriksson and Wich, 2006). Spatial synchrony between populations was also linked to the synchrony of weather conditions during important phases of the reproductive cycle (Moran effect) (Koenig, 2002). Synchrony of trees within the same population was modeled using the standard deviation (SD) between individual seed production in any given year (e.g., Isagi et al., 1997). At the individual level, pollen availability is a key control on synchrony within populations ("pollen coupling"), even if such a link has been modeled only by theoretical formulations so far (Satake and Iwasa, 2000, 2002a,b; although see Bogdziewicz et al., 2017b).

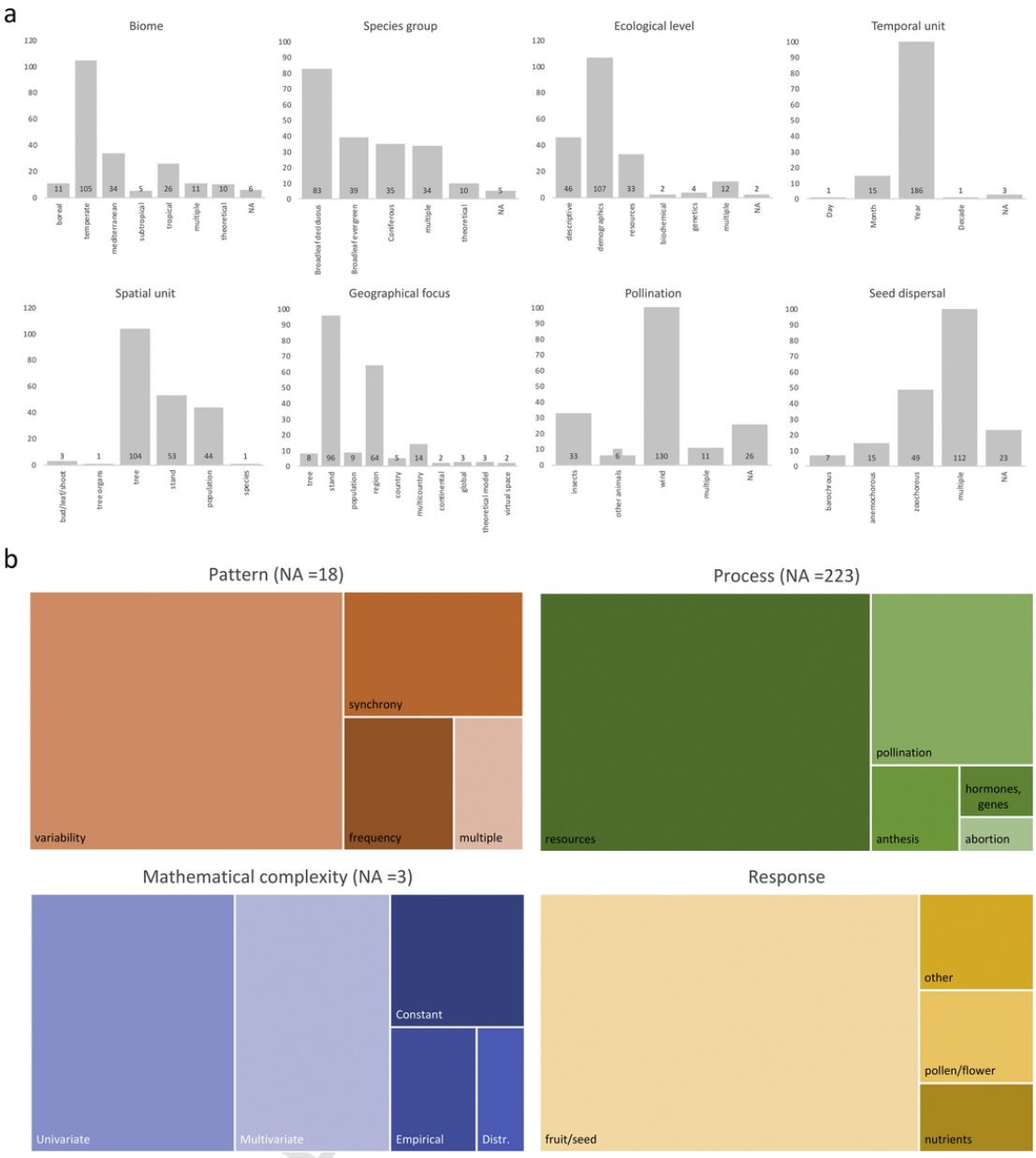


**Fig. 4.** Number of papers (a) and formulations (b) for each categorical variable addressed in the present review.

Frequency was the least reported pattern of masting. Measures of frequency included a typical (mean) return interval, or a typical frequency, of mast years (Hilton and Packham, 2003; Nussbaumer et al., 2016). This approach relies on the identification of a binary threshold for masting (i.e., the definition of a mast year vs. a non-mast year). Most models included in Table 1 characterized masting patterns by frequency. A more rigorous approach is to conduct a form of spectral analysis such as Fourier analysis, but this was not frequently reported (Abrahamson and Layne, 2003; Kasprzyk et al., 2014). A similar approach is to test for temporal autocorrelation at different timescales (Greene and Johnson, 2004). Spearman's rank correlation between seed production series over different periods also seems to be a good estimator to test for variations in frequency (Allen et al., 2012; Greene and Johnson, 2004).

### 3.2. Processes

Excluding studies with simple weather or climate correlations, only 100 formulations out of 323 explicitly modeled a masting process. Most of these were empirically based (76%) and stand-alone (83%), confirming a significant lack of implementing masting within larger model frameworks. Our review has confirmed the stronger tradition of studies related to resource acquisition, storage and allocation, which represented the most abundant (67%) and longest-studied group (Table 3). Pollination (22%) has come under the focus of research more recently, whereas studies on floral induction-anthesis (6%), hormonal and genetic regulation of bud formation (3%), and seed maturation after flower abortion (2%) have been emerging as a novel yet challenging approach.

Our review also highlighted the fact that efforts to relate seed production to multiple and interacting proximate causes were more frequent for pollination (50%) and resource-related studies (45% of for-

**Table 3**
Formulations on masting processes and their proximate causes.

| | Number of formulations | Range of publication dates |
|---|---|---|
| Resources | 67 | 1987–2016 |
| Hormonal and genetic regulation | 3 | 2012–2013 |
| Pollination | 22 | 1998–2016 |
| Seed maturation, flower abortion | 2 | 2002–2012 |
| Flower induction, anthesis | 6 | 2010–2016 |
| **Total** | **100** | |

mulations), as opposed to only 27% of those using hormonal, genetic, or flowering processes (Table 4).

Only 83 formulations addressed both a pattern and a process of masting. The review of such simultaneous pattern and process formulations highlighted the complex relations among them (Fig. 5). No process could explain individually the variability, synchrony or frequency of masting, but rather a combination of processes was always involved in all patterns (Crone and Rapp, 2014; Pearse et al., 2016).

### 3.3. Examples of masting process formulations

Three-quarters of studies on masting processes (i.e., 73 papers) focused on broadleaf species. To illustrate how masting patterns and processes can be modeled, we collected formulations for species belonging to the *Fagales* order (Table 5), which have been repeatedly analyzed by some of the most recent and comprehensive studies on masting. These formulations differ from what exposed for forest models that did / did not include masting (Table 1) in that they are stand-alone analyses that have usually been subject to validation against empirical measurements.

## 4. Challenges for modelling masting

### 4.1. Options to implement masting in forest models

Based on the review of 206 papers on the use of mast seeding in forest models, we confirmed that masting is an important albeit overlooked process in modelling forest dynamics. The review highlighted the progression in understanding of masting by ecologists, from the description of temporal variability in seed production, to a more mechanistic understanding of what drives the highly fluctuating and synchronous seed production at the population level.

Different options are available to "reproduce reproduction" in forest models for masting species, from very simple (formulations for variability, synchrony, frequency) to semi-empirical (seed crop as a function of weather) or completely detailed (explicitly accounting for resources, hormones, and genetic regulation). Complete process-based approaches should have the capability of producing emergent masting patterns without the need to parameterize them externally. However, while it may seem desirable to improve model realism by including a

**Table 4**
Mathematical complexity of process formulations by process category in the reviewed studies.

| Mathematical complexity | All | Resources | Hormonal and genetic regulation | Pollination | Seed maturation | Flower induction, anthesis |
|---|---|---|---|---|---|---|
| Constant | 4 | 3 | – | 1 | – | – |
| Distribution | 2 | – | – | 2 | – | – |
| Univariate | 47 | 31 | 2 | 8 | – | 6 |
| Multivariate | 45 | 31 | 1 | 11 | 2 | – |
| NA | 2 | 2 | – | – | – | – |
| **Total (formulations)** | **100** | **67** | **3** | **22** | **2** | **6** |

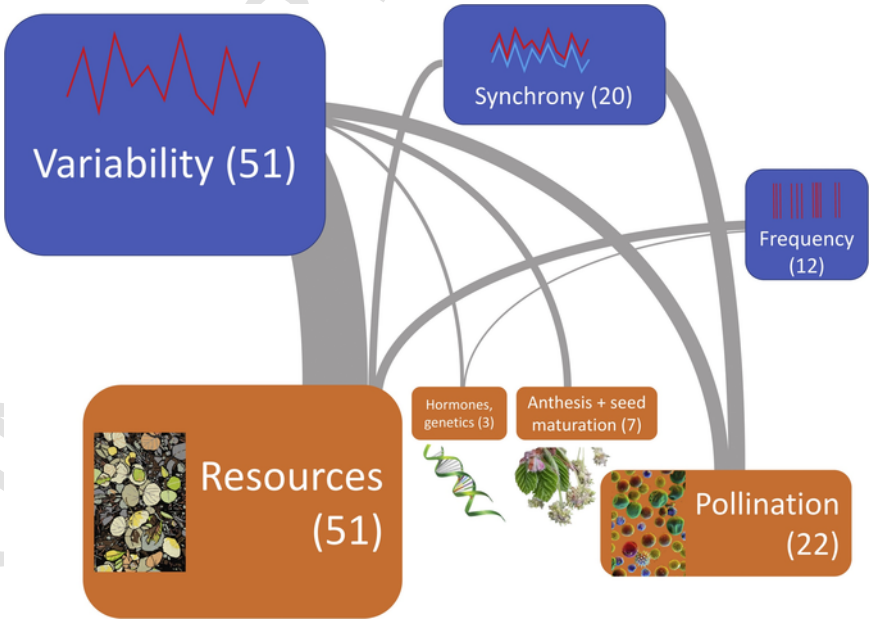


**Fig. 5.** Links between patterns and processes of masting in 83 reviewed studies addressing both types of formulations (number of studies in brackets). The size of boxes and connectors is proportional to the number of studies found.

**Table 5**
Examples of masting formulations (patterns and processes) for the *Fagales* order.

| Pattern | References | Species | Formulation |
|---|---|---|---|
| Variability | Pesendorfer et al. (2016) | *Quercus lobata* | Coefficient of variation of individual tree crop size across time = 74.9%–457.0%<br>Coefficient of variation of mean relative crop size of all trees across time = 91.5%<br>Lag-1 autocorrelation of mean seed production of all trees in the population = −0.53 |
| Synchrony | Pesendorfer et al. (2016) | *Quercus lobata* | Mean cross-correlation of seed production among all trees in the population = 0.49 (range: 0.41–0.55) |
| Frequency | Nussbaumer et al. (2016) | *Fagus sylvatica, Quercus robur, Q. petraea* | Mast frequency (number of years of observations/number of years with masting) = 2.6–5.50 for beech and 2.11–6.33 for oaks |

| Process | Reference | Species | Formulation | Goodness-of-fit |
|---|---|---|---|---|
| Resource availability | Miyazaki et al. (2014) | *Fagus crenata* | Relative flowering intensity in next spring [0–1] = –1.27 + 1.20 (N% dry matter) | r = 0.78 |
| Resource allocation and storage | Han et al. (2008) | *Fagus crenata* | N content (mg) of winter buds containing both leaf and flower primordia formed in a masting year were 2.1–3.4-fold higher than in winter buds containing leaf primordia only. | F = 67.97, p < 0.0001 |
| | Hoch et al. (2013) | *Carpinus betulus, Fagus sylvatica and Quercus petraea* | $\delta^{13}C$ % in flowers after 8 years $CO_2$ enrichment at 530 ppm was 0.95–1.14 times that at ambient CO2 | p (t) < 0.1 |
| | Hoch and Keel (2006) | *Carpinus betulus and Fagus sylvatica* | δ13C % in fruits and vegetative infructescence tissue after girdling or defoliation was respectively 0.58–0.99 and 0.16–0.97 times the control | p (t) < 0.1 |
| Hormonal/ genetic regulation | Miyazaki et al. (2014) | *Fagus crenata* | Relative flowering intensity in next spring [0–1] = 0.15 + 0.33 (FcFT relative expression in July) | r = 0.86 |
| | | | FcFT relative expression in July increased 14.6 times under fertilization with the addition of 4.6 g N $m^{-2}$ month-1 between April and August of the previous year | p < 0.001 |
| Pollination | Pesendorfer et al. (2016) | *Quercus lobata.* | Each tree obtains a fixed amount of surplus energy (Ps) from photosynthesizing, and when the stored energy surpasses a threshold (Lt), the surplus (Cf) is invested in flowers. The pollinated flowers then bear fruit (Ca), whose production cost (Rc) is proportional to the number of flowers, so that Lt–Ca = Lt–Rc Cf.<br>Ca is then scaled on mean daily TMax of April, which is a proxy for phenological asynchrony:<br>Ca = 0.01 Rc Cf (100–10*(8.9 – TmaxApril0)) | r = 0.43 |
| | Bogdziewicz et al. (2017a)[a,b] | *Quercus ilex.* | ln (seed production) = 4.86<br>–0.11 length $_{ps\ year\ 0}$<br>–0.32 pollen abundance<br>–1.10 spring $_{year\ 0}$ WD<br>+0.79 Precip $_{January\ 0–June\ 0}$<br>+0.21 seed production $_{year}^{-1}$<br>+0.28 length ps $_{year}^{-1}$<br>+0.14 spring $_{year}^{-1}$ WD<br>−0.97 length ps0 x spring 0 WD<br>+0.58 length $ps_0$ x length $ps^{-1}$<br>+0.54 spring0 WD x spring $^{-1}$ WD | Variance explained = 61% |
| | Pearse et al. (2015) | *Quercus lobata* | (a) Pollen exclusion decreased acorn density by 70% compared to open-pollinated controls; (b) pollen supplementation increased acorn crop by 125% | (a) F1,29 = 9.4, p = 0.004, (b) F1,29 = 7.8, p = 0.009 |
| Seed maturation | Tsuruta et al. (2011) | *Quercus serrata* | Beyond 80 days after pollination (late July), the survival of acorns from artificial self-pollination and non-pollination treatments was 90–100% lower than under outcross-pollination | t = 4.79<br>df = 5<br>p = 0.00497 |
| Weather cues | Vacchiano et al. (2017) | *Fagus sylvatica* | Logit (masting class [1–5]) = −1.25 Masting $class_{year\text{-}1}$ +0.55 $Precipitation_{June\text{-}2}$ +1.27 $TMax_{July\text{-}1}$ −1.05 $Tmax_{July\text{-}2}$ +0.75 $TMax_{June\text{-}1}$ | $R^2$ = 0.53–0.65 |
| Weather vetoes | Bogdziewicz et al. (2017a)[a,b] | *Quercus ilex* | ln (seed production) = 4.12 | Variance explained = 0.68 |

**Table 5** (*Continued*)

| Process | Reference | Species | Formulation | Goodness-of-fit |
|---|---|---|---|---|
| | | | +0.19 mean $TMax_{pollen\ season0}$<br>+0.19 $TMax_{ps}^{-1}$<br>+0.15 daily $Precip_{ps0}$<br>–0.76 daily $Precip_{ps}^{-1}$<br>+1.44 Precip January 0–June 0<br>–0.12 seed $production_{year}^{-1}$<br>+0.57 Tmaxps 0 x $TMax_{ps}^{-1}$<br>+0.55 seed $production_{year}^{-1}$ x Precip January 0–June 0 +0.77 $TMax_{ps0}$ x $Precip_{ps}^{-1}$ | |

[a] standardized regression coefficients.
[b] WD = water deficit, ps = pollen season.

higher number of processes, this would also increase model complexity and introduce more sources of uncertainty.

Regarding model complexity, it is clear that proximate causes of masting involve different ecological levels and occur at several scales (from leaf to stand). This presents a challenge for models that operate either at the wider side of the scale spectrum, because they may miss the processes that result in emergent masting behavior, or at the narrower, because process modeled with insufficient accuracy or complexity may fail to generate the desired pattern when the model is up-scaled.

Regarding model uncertainty, while some masting processes have been repeatedly described by quantitative algorithms (e.g., resource uptake, allocation and storage), other processes are fairly unclear. For example, if masting needs to be modeled in a process-based way, flowering and pollination should be addressed by algorithms and included either implicitly or explicitly in forest models. So far, only little evidence has been elaborated on the interaction between resource dynamics in the tree and biochemical processes, which renders the implementation of this masting component difficult in forest models. Additionally, nutrient cycles are missing from many forest models (especially P), or may have not been validated as thoroughly or extensively as other process (e.g., Vega-Nieva et al., 2013). The uncertainty on such a crucial mechanism of masting both in the masting literature and in its implementation in forest models calls for more scientific effort. On the other hand, hormonal and genetics components, which operate as a signaling device, are usually not included explicitly in forest dynamics models, especially when the modelling object is larger than a single tree.

For these reasons, modeling masting by patterns (variability, synchrony, or frequency) rather than processes might be the best option currently available for those forest models that operate at spatio-temporal scales incompatible with a process-based implementation of the main masting processes (e.g., "big leaf" global dynamic vegetation models), or when the variables involved are not readily produced by the model or when data to parameterize a process-based formulation are lacking.

When several formulations of masting patterns and processes are available for some species or biome, the choice of which to include in a forest model depends on the predictor and response variables involved, and on the temporal and spatial resolution of the other model components (e.g., tree vs. stand). The large amount of empirical studies and data accumulated in the literature (e.g., Mencuccini et al., 1995; Schauber et al., 2002; Ascoli et al., 2017) should nevertheless represent a solid base to calibrate masting formulations for many species, biomes, and ecological resolutions, but a minimum number of temporal and spatial observations needs to be assured. Although we have reported examples of masting algorithms for some species and biomes (Table 5), modelers operating in different or novel ecosystems should be cautious when assuming that process-based masting models would work in the same way there. Indeed, some of the mechanisms underlying proximate causes of masting may be highly context-dependent (e.g., significant weather predictors), although the scale at which they vary is not entirely clear yet (Vacchiano et al., 2017). On the other hand, even in the absence of calibration data, quantifying the variability, synchrony, and frequency of masting that emerge from process-based models of seed production may serve as a tool for the verification of model behavior.

### 4.2. Linked patterns, linked processes

Even if pattern-only formulations are used, the strong relationships between such patterns need to be acknowledged. For example: high variability at the population scale is only observable when synchrony is high (Koenig et al., 2003); synchrony is only meaningful if measured over a long period of time (one year's high synchrony is not enough to define masting); finally, the frequency of mast events is an indirect component of their variability, since rare high seed production events also imply a relatively high variability. Any quantitative description of mast seeding therefore needs to combine the temporal and the spatial dimensions of all masting patterns (Fig. 2).

Likewise, a process-based formulation must take into consideration that masting is determined by a chain of events (Fig. 3). More tests with existing or new forest models are needed to understand whether all such processes must be included to obtain an accurate simulation of mast seeding, and to assess the trade-offs between realism gained and uncertainties introduced when chaining several sub-models together.

An example of successful model chain is represented by Resource Budget Models (RBM) (Isagi et al., 1997), which include a strong link among most of the proximate causes of masting. In particular, resource allocation and depletion and pollination processes (pollen coupling combined to density-dependent pollen limitation) are linked in RBM, because pollen availability depends on the amount of resources allocated to flowering (both male and female flowers). In particular, the RBM postulates that that: (i) a plant cannot gain the amount of resources required to produce a high seed production in one year only, but needs to accumulate resources over multiple years until its resources exceed some threshold that allows them to reproduce; (ii) the ratio between the amount of resources used for fruiting and those used for flowering regulates masting patterns, i.e., a higher ratio results in a higher inter-annual variability and lower frequency; (iii) a large seed crop causes resource depletion for the individual plant, which will fail to reproduce in subsequent years as long as its reserves are below the threshold (Fig. 6). Theoretical RBM produce an emergent representation of variability and synchrony of masting (Rees et al., 2002; Satake and Iwasa, 2002a,b; Venner et al., 2016); noise in synchrony between individuals and populations is taken into account by varying the level of resources gained by each tree and each year through photosynthesis.

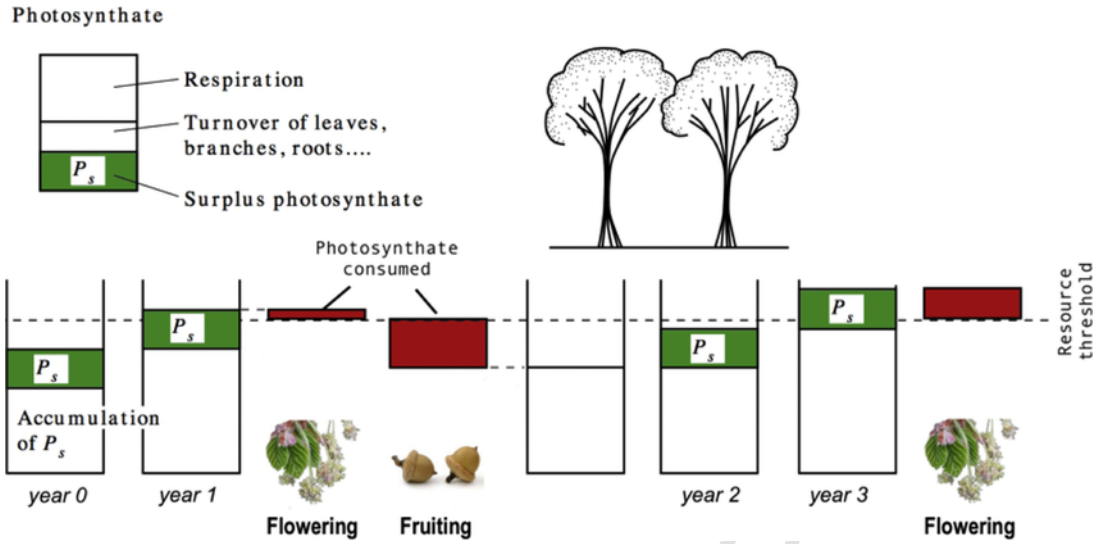


**Fig. 6.** Conceptual structure of a Resource Budget Model for masting (adapted from Isagi et al., 1997).

Yet, RBMs have been tested empirically for very few species (see Crone and Rapp, 2014 for a review). For example, it is unclear if the resource whose accumulation and depletion are simulated in RBM is carbon (NSC) or rather some less abundant nutrient such as N or P. In addition, Pearse et al. (2016) questioned the existence of a resource "threshold" for reproduction. Should such a threshold exist, most species would have no reproduction in most years–a hypothesis that lacks empirical confirmation (Monks and Kelly, 2006; Kelly et al., 2013) as seedfall is often continuously distributed (Kelly, 1994; Koenig and Knops, 2000; Allen et al., 2012).

A proposal for a novel process-based implementation of masting within forest models could therefore revolve around validating and improving RBMs, possibly integrated with the knowledge collected about pollen regulation from a biochemical context, dynamics of limiting resources, and weather influences on both resources and pollination processes as a trigger or signal (Fig. 7). Such implementation would also provide grounds to test hypotheses on the ecological relevance of masting (e.g., after natural disturbance: Ascoli et al., 2015) and about the effect of climate change on masting and its patterns, a topic which is still largely controversial due to the interactions between different processes and variables involved (McKone et al. 1998; Piovesan and Adams, 2001; Jump et al., 2006; Övergaard et al., 2007; Drobyshev et al., 2010).

Future research on this topic will need to focus on understanding the most important controls of the masting process cascade, moving away from a "big bucket" approach and focusing on proximate causes still lacking a formal quantitative treatment (e.g., hormonal induction, resource allocation), while trying to link with inputs and outputs currently used by forest models. Also, variation in masting patterns and processes between species/biomes will need to be better understood, with a special focus on less known ecosystems (e.g., tropical). A suitable design to advance these ideas and calibrate predictive models would involve the experimental manipulation of resource dynamics at various life stages of the tree. In particular, this would address the reproductive cycle, with complementary measurements of inter-annual variation in climate and resources, as well as reproductive buds, flowers and seeds (Allen et al., 2017). In addition, the design would account for contrasts between functionally different species in the same environment, and for the same species in markedly different environments.

## Authors' contribution

GV coordinated and conceived the study, with the contribution of all authors during a COST workshop in Turin, Italy. All authors carried out equal parts of the literature review, and contributed to the outline of the manuscript and to the figure concepts during a COST workshop in Cambridge, UK. GV and AHP analyzed the data; PM, ES, and TW compiled the tables; DA, MELB, TC, TW, and GV drew the figures. All authors contributed to discussion of the results and the writing of the manuscript.

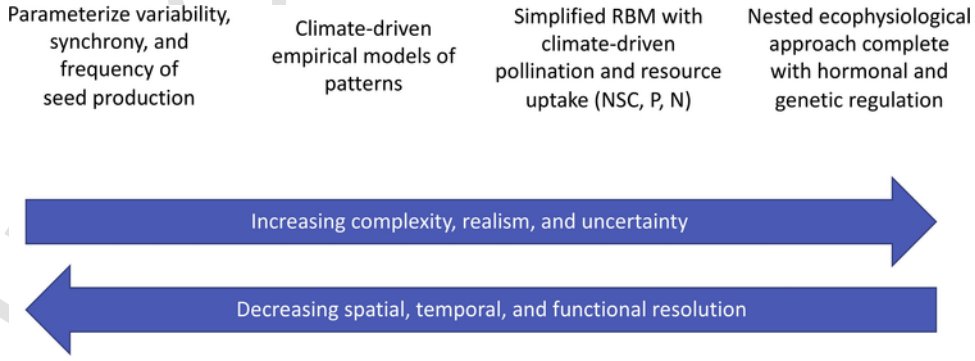


**Fig. 7.** Recommendations to include masting in forest models as a function of model resolution and complexity.

## Uncited references

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.03.004.

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